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Genetics and Biogeography of the *Oeneis chryxus* Complex (Satyrinae) in California

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Abstract. The nominal taxa *Oeneis ivallda* Mead and *Oe. chryxus stanislaus* Hovanitz are alpine butterflies endemic to the Sierra Nevada of California. The range of *Oe. c. stanislaus* is entirely contained within the range of *Oe. ivallda*. The two intergrade gradually in the north and abruptly in the south, and electrophoretic-genetic analyses fail to demonstrate any interruption in gene flow between them. This is consistent with the interpretation that *ivallda* and *stanislaus* are forms of a single species, and we recommend they be classified as subspecies of *Oe. chryxus* Doubleday and Hewitson pending comparisons with Rocky Mountain *Oe. chryxus chryxus*. Hovanitz's (1940, Ecology 21:371) hypothesis that the color morphs are maintained by selection for crypsis breaks down in the northern Sierra, where the pale *ivallda* morph is often found on dark substrates.

The peculiar distribution of these taxa suggests a double invasion of the Sierra, with *stanislaus* having arrived secondarily from the east across the Great Basin. We discuss the plausibility of the easterly colonization route, which remains controversial in the botanical literature. Further genetic investigation of the *chryxus* complex may provide a definitive test of this hypothesis.

Introduction

Oeneis ivallda Mead, a pale, sometimes nearly white Satyrine butterfly ranging from Nevada to Inyo and Tulare Cos. in California, is the only truly endemic butterfly to reach both the north and south alpine limits of the Sierra Nevada. Its biogeographical relationship with what is presently called *Oeneis chryxus stanislaus* Hovanitz has posed an evolutionary problem now recognized for over 50 yr. This relationship bears in turn on the origin of the alpine biotic community in this mountain range. *Oe. chryxus stanislaus* was described by Hovanitz (1937) from Sonora Pass, Alpine Co. It does not differ from *Oe. ivallda*

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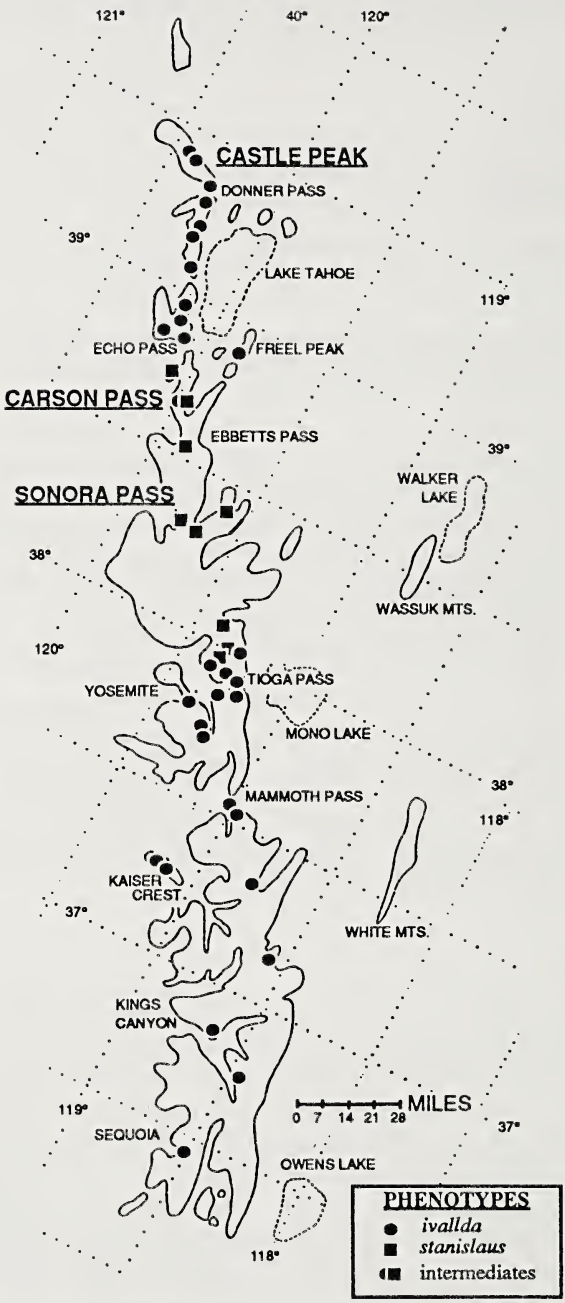

Fig. 1. Distribution of alpine habitats in the Sierra Nevada of California with known localities of *Oeneis ivallda* and *Oe. chryxus stanislaus*, redrawn from Hovanitz (1940) with additional confirmed localities added. Populations sampled in this study are in the larger sized font.

in genital morphology, indeed, the only basis for diagnosis is color, both sexes being a deep "butterscotch" brown. The geographic distribution of *stanislaus* was documented by Hovanitz (1940); it is entirely contained in the central Sierra, from Carson Pass to Tioga Pass, with pure *ivallda* distributed parapatrically to the N and S. His map is updated and reproduced here (Fig. 1). The darkest *stanislaus* occur around Sonora Pass, with a gradual decrease in the frequency of dark phenotypes N-ward to only ~5% at Carson Pass (AMS, unpublished data) and 0% near Donner Pass, but an abrupt transition zone to the S "showing the entire range of variation from darkest to lightest" near Tioga Pass (Hovanitz 1940, p. 371). This appears to be a unique geographical relationship, not reproduced in any pair or set of taxa in the Sierran flora, for example (G. L. Stebbins, *pers. comm.*). Virtually the same phenomenon has been reported in Andean birds, however, under the rubric "leapfrog variation" (Remsen 1984). In the cases discussed by Remsen, the N and S populations are treated as two geographic subspecies, separated by a third, more distinct subspecies.

By 1940 Hovanitz had become convinced *ivallda* and *stanislaus* were in fact conspecific, although authorities subsequent to Hovanitz have differed in their treatments. These authorities based their judgment on inexplicit criteria, without any new biological data to justify them. Garth and Tilden (1963) combined both names under *ivallda* as a single subspecies of the widespread boreal and Rocky Mountain species *chryxus* Doubleday and Hewitson. The same authors treated them as separate species 23 yr later (*Oe. ivallda* and *Oe. chryxus stanislaus*; Garth and Tilden 1986), as did Tilden and Smith (1986) and Miller and Brown (1981). Emmel (1975) also kept them separate, but Scott (1986) recognized both as subspecies of *chryxus*. The difference in wing-pigment chemistry, the only diagnostic character reported to date, is not in itself a basis for recognizing biological species, especially when the color phenotypes intergrade. One way to approach the question of species status independently is to look for biochemical-genetic evidence indicating an interruption of gene flow (discussed below).

The *ivallda/stanislaus* problem is interesting from a biogeographic as well as taxonomic standpoint because the localization of *stanislaus* in the central Sierra appears discordant with models of colonization from the N but potentially concordant with immigration from the E, as recognized by Hovanitz (1940):

"It may be postulated (1) That the Sierra Nevada was once entirely populated by a white race and that the brown race has either originated *de novo* in the central part or that it has come in via the high Basin Ranges from other populations of the brown form; (2) that the Sierra Nevada was once populated entirely by a brown race at either end of which genes for whiteness developed greater concentrations, or (3) that a uniform population never did exist in the Sierra Nevada (p. 373)."

Hovanitz notes correctly that all the Rocky Mountain populations of

chryxus are brown, and claims that "Individuals from these populations could more easily reach the Sierra Nevada via the high Basin Ranges which form a series of 'stepping-stones' across the uninhabitable desert areas . . . than any other way."

Because the Sierra Nevada is a young range, with most of the major deformation leading to the modern fault-scarp topography occurring only in the past 3 MY (Bateman and Wahrhaftig 1966) — corresponding with the first evidence of glaciation (Curry 1966) — the origin and evolution of the Sierra Nevada alpine biota represents a relatively recent event. For this reason, it has received the attention of historical biogeographers and community ecologists interested in the evolution of new biotas. The conventional wisdom regarding the origins of the Sierran alpine biota strongly favors a strictly northerly route of colonization of alpine/boreal taxa (such as *Oeneis*) (Sharsmith 1940, Axelrod 1957, 1977; Chabot and Billings 1972), although many endemic plant species evolved *in situ* from dry-adapted continental taxa widespread at lower altitudes (Stebbins and Major 1965).

Scenarios have been promoted involving easterly immigration of some small proportion of the alpine biota from the Rocky Mountains (Harshberger 1911; Major and Bamberg 1967; Major and Taylor 1977), despite objections in the literature (Axelrod 1976). Although the sequence of glacial events and the interglacial vegetation in the Sierra Nevada remains very sketchy (Fullerton 1986), Wells (1983) published data from wood rat (*Neotoma*) middens demonstrating the presence in SE Oregon in full-Wisconsinian glacial time of a prostrate juniper steppe with patterned ground, even below 1500 m. It is not difficult to visualize *Oeneis chryxus* living in such a climate. Wells considers that the low elevation desert trough E of the central Sierra has constituted a major barrier to the W-ward dispersal of Rocky Mt. organisms. The possibility that such organisms came in from the NE (N Great Basin) along the shores of the pluvial lakes, spreading into the Sierra at lower elevations initially on the E flank, must be taken seriously. At least one "easterly" scenario has been borne out: Major and Bamberg's (1967) prediction that *Pinus flexilis* (Pinaceae) would be found to have spread to the Sierra from the E in the Mojave sector has been amply validated by Wells' *Neotoma* data.

The biogeographical and evolutionary-ecological framework for interpretation of the *ivallda/stanislaus* problem differs depending on whether one is dealing with one species or two. As a single species, both forms could have arrived in a polymorphic population colonizing from the N or E; as separate waves of colonists from the same or different directions; or one form could have arisen and spread within the Sierra. The relevant evolutionary questions would involve the biogeography of diagnostic characters alone. This was the type of question addressed by Hovanitz (1940) when he claimed that visual selection for background matching (crypsis) by predators would favor the pale

ivallda morph on granitic substrates and the darker *stanislaus* morph on andesite, and that the geography of the colors matched that of the substrates. If the two forms belong to two species, one might interpret the situation as one of competitive exclusion of *ivallda* by *stanislaus* in the central Sierra; the most interesting questions would address the whole genomes of these taxa from the perspective of community ecology — for example, "What ecological factors limit *stanislaus* to the central part of the high Sierra?" Here, we attempt to test the assumption of conspecificity using electrophoretic characters, in an attempt to refine evolutionary and biogeographical investigations to the proper level of analysis.

Materials & Methods

Three samples were available for this study (Fig. 1): from the ridge between Castle and Basin Peaks, Nevada Co., 2.VII.1989 (*leg.* AMS) (phenotypically pure *ivallda*, no *stanislaus* or intermediates ever recorded in 18 yr) (n = 20); Carson Spur along Hwy. 88, Alpine Co., 4.VII.1989 (*leg.* J. Mori) (mostly *ivallda*, approximately 5% intermediate in long series, occasionally approaching full *stanislaus* in color) (n = 19); and Sonora Pass, Alpine-Tuolumne-Mono Cos., 5.VII.1989 (*leg.* J. Mori) (phenotypically pure *stanislaus*) (n = 19). All individuals were frozen alive at −80°C. The heads and thoraces were homogenized for analysis; all wings and genitalia were retained as vouchers deposited in the Bohart Museum of Entomology at Davis. Every individual was scored as *ivallda*, intermediate, or *stanislaus* independently by both of us; only two individuals (from Carson Spur) were ambiguous (scored as intermediate by one of us, *ivallda* by the other).

Electrophoresis protocol followed Ayala et al. (1972) and Geiger and Shapiro (1986), as modified by Porter and Matoon (1989). 16 loci were studied: adenylate kinase (AK-1; Enzyme Commission number: 2.7.4.7), aldolase (ALDO; 4.1.2.13), glucose-6-phosphate dehydrogenase (G6PD; 1.1.1.49), glutamic-oxaloacetic transaminase (two loci: GOT-1, GOT-2; 2.6.1.1), glyceraldehyde-3-phosphate dehydrogenase (GAPDH; 1.2.1.12), α-glycerophosphate dehydrogenase (α-GPD; 1.1.1.8), hexokinase (HK-1; 2.7.1.1), isocitrate dehydrogenase (IDH-1; 1.1.1.42), malate dehydrogenase (MDH-1, MDH-2; 1.1.1.37), malic enzyme (ME-1, ME-2; 1.1.1.40), phosphoglucose isomerase (PGI; 5.3.1.9), phosphoglucomutase (PGM; 2.7.5.1), and the anodally migrating locus of superoxide dismutase (SOD-2; 1.15.1.1). Zymograms were scored using letter designations, with the fastest allele in the cathodal direction given the letter A. Data were analyzed using the computer program BIOSYS-1 (Swofford and Selander 1981). Formulae for the basic population genetic parameters used here are given and discussed in most introductory population genetics textbooks (e.g., Hedrick 1985) and will not be repeated here. The banding patterns are entirely consistent

Table 1. Allelic frequencies at variable loci.

Locus & allele	Population (*ivallda*) Castle Peak[a]	(*ivallda* + intermediates) Carson Spur[b]	(*stanislaus*) Sonora Pass[c]
AK-1			
A	0.950	0.947	0.947
B	0.050	0.053	0.053
GAPDH			
A	1.000	0.947	1.000
B		0.026	
GOT-1			
A		0.079	0.079
B	0.975	0.842	0.605
C	0.025	0.026	
D		0.053	0.316
α-GPDH			
A	1.000	0.974	1.000
B		0.026	
HK			
A	0.150	0.211	0.071
B	0.850	0.789	0.929
IDH-1			
A	0.100	0.053	0.105
B	0.100	0.105	0.105
C	0.375	0.500	0.553
D	0.425	0.316	0.237
E		0.026	
ME-1			
A		0.026	0.179
B	1.000	0.947	0.821
C		0.026	
PGI			
A	0.375		
B	0.550	0.868	1.000
C	0.075	0.132	
PGM			
A	0.625	0.447	0.263
B	0.375	0.553	0.737

[a] n = 20. [b] n = 19. [c] n = 19, except n = 14 at HK & ME-1.

with those expected from segregating alleles of mono-, di-,and tetrameric enzyme systems reported for these loci in other organisms (Harris and Hopkinson 1976; Kitching 1985). Since no breeding program has been carried out, we made the usual assumptions in treating electromorphs as alleles for the purposes of genetic analysis.

Table 2. Genetic variability in sample populations. A: mean alleles per locus, H_{obs}: observed proportion of heterozygotes, H_{exp}: heterozygote proportions expected from Hardy-Weinberg ratios, P: percent of loci polymorphic, with more than one allele detected. Standard errors in parentheses.

Population	A	P	H_{obs}	H_{exp}
Castle Peak	1.6 (0.2)	37.5	0.128 (0.054)	0.133 (0.058)
Carson Spur	1.9 (0.3)	56.3	0.138 (0.048)	0.146 (0.051)
Sonora Pass	1.6 (0.2)	37.5	0.146 (0.060)	0.132 (0.054)

Results

Allelic frequencies for the nine variable loci are given in Table 1; the remaining loci (ALDO, GOT-2, G6PD, MDH-1, MDH-2, ME-2, and SOD-2) were monomorphic. We found no deviations from Hardy-Weinberg proportions. Genetic variability scores for all populations are shown in Table 2. These values are in the normal range for most invertebrates (Thorpe 1983), including butterflies (AHP, AMS, and HJ Geiger, *unpubl.*), indicating that there is enough genetic variability available to permit differentiation of these populations (and taxa) in the absence of gene flow. Indeed, χ^2 contingency table analyses indicate statistically significant differences in allelic frequencies among populations at four of the nine variable loci (GOT-1: $p < 0.0003$; ME-1: $p < 0.02$; PGI; $p < 0.00001$; PGM; $p < 0.006$). However, analysis using F_{ST} (Wright 1931) indicates that despite statistical significance, this degree of differentiation is biologically minor (GOT-1: $F_{ST} = 0.133$; ME-1: $F_{ST} = 0.083$; PGI: $F_{ST} = 0.212$; PGM: $F_{ST} = 0.088$; other variable loci: $F_{ST} < 0.03$; mean $F_{ST} = 0.081$).

The weak differentiation among populations is perhaps reflected in a more familiar way by the low genetic distances (Fig. 2). Using UPGMA as a clustering algorithm (Sneath and Sokal 1973), eight of ten independent analyses grouped Carson Pass (mostly *ivallda* by wing color) with Sonora Pass (*stanislaus*), white the other two grouped Carson with Castle Peak (*ivallda*). Notably, the distance between nodes in these analyses was small, and the greatest genetic distance shown was always within the range shown by subspecies or consubspecific populations in other animal groups (Thorpe 1983). There was nothing to suggest the interruption of gene exchange expected across a species boundary. Taken together, the genetic analyses indicate that (i) the Carson Pass population is more intermediate than wing color data would suggest, and (ii) these populations are only weakly differentiated.

Discussion

Genetic population structure and species-level taxonomy. — There is nothing in our data which would suggest that the *ivallda* and *stanislaus*

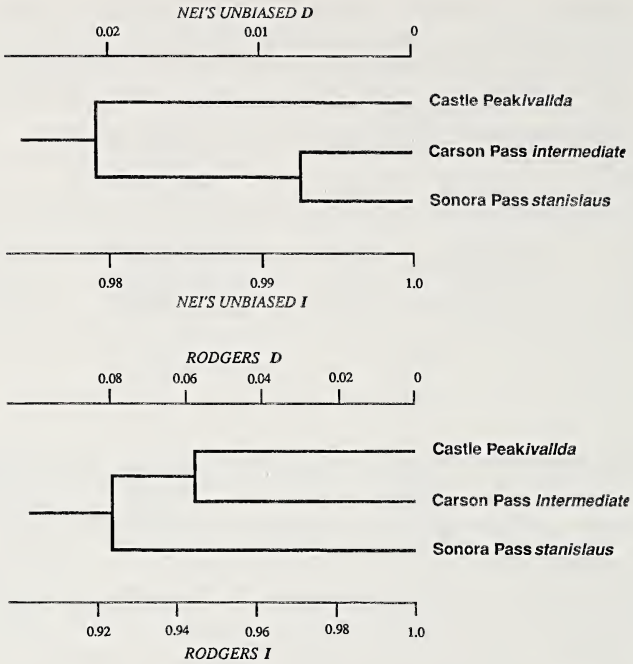

Fig. 2. Genetic distance (Nei 1978, Rodgers 1972) phenograms clustered using UPGMA (Sneath and Sokal 1973). The distances shown are well within the ranges exhibited by subspecies in most butterflies studied. Their lack of concordance indicates the close relationship between these populations.

populations belong to separate species. We found intermediate wing color phenotypes, no diagnostic enzyme loci, and no consistent clinal patterns from locus to locus. At the same time, it must be stressed that analyses of electrophoretic data are logically designed to detect interruption of gene flow. Failure to detect such interruption is not equivalent to demonstrating that gene flow is occurring, because very similar allelic distributions could conceivably be generated by parallel stabilizing selection even in the absence of gene exchange. However, alternative scenarios which do not invoke gene flow become less probable as more loci are examined and found with high similarities: each enzyme locus is likely to respond differently to selection pressures (Carter and Watt 1988), but all loci respond similarly to gene flow.

By assuming that selection on enzyme alleles is weak when averaged over loci, and with the knowledge that genetic drift inescapably differentiates populations, we can use population genetic theory to generate a simplest-case scenario to explain the observed genetic similarity in terms of gene flow. This scenario represents a most-parsimonious hypothesis which can potentially be falsified with data from additional

enzyme loci, with knowledge of the responses to selection by the alleles at sampled loci, or with evidence of geographic variation in previously undetected alleles. If the gene flow estimate we generate is high, then the populations are conspecific under the most parsimonious interpretation of the data.

Under an infinite island model with no selection, the F_{ST} scores we report are explainable by genetic drift counteracted by an average gene exchange rate of approximately 2.8 individuals migrating between these populations each generation (using Wright's [1931] formulation $Nm \approx (1/F_{ST} - 1)/4$, where Nm is the rate of gene exchange among populations). This gene flow rate is sufficiently strong to unite the gene pools of these populations (Wright 1931). However, the infinite island model of population structure seems unrealistic for *Oeneis*. We have observed "hilltopping" behavior (Shields 1967) in both *ivallda* and *stanislaus*: males aggregate on mountain peaks and ridges in search of receptive females. This mating system and the relative continuity of the alpine habitat (Fig. 1) imply that these butterflies are distributed among geographically adjacent or semi-connected populations, and are better described using an isolation-by-distance model of population structure. When sampled populations are separated by intervening populations in an isolation-by-distance model (as here), then the gene flow estimated from F_{ST} represents the average rate of genes diffusing between the sampled populations — the rate of individual animals actually exchanged is a function of the distance between samples, and can be much higher between adjacent local populations (Slatkin and Barton, 1989). Thus, under a model of genetic population structure which seems realistic for these butterflies, gene flow between these taxa is likely to be only weakly interrupted at best.

Although *Oeneis* seem ideal for mark-recapture experiments, no estimates of individual dispersal are presently available to compare against our estimates from genetic data. Garth and Tilden (1963, p. 77) document the ability of *ivallda* to colonize an unusual habitat 300 m lower in elevation than others. AMS visits Donner Pass (2100 m), 2 km from Castle-Basin Peak, regularly during *Oeneis* flight season and has observed two individual *ivallda* there in 18 yr (1 male, 1 female), a high enough incidence to suggest fairly frequent dispersal beyond the alpine zone. The distribution of *Oeneis* in W Nevada (discussed below) also suggests the ability to move among habitat patches.

Taxonomists often assume that characters diagnostic of parapatric or allopatric taxa are indicative of more fundamental genetic differentiation. If Hovanitz's (1940) scenario is correct, the two *Oeneis* color morphs are maintained by selection for crypsis on different substrates. Such a selection differential will erect a partial barrier to the flow of genes between them (Barton 1979, 1983). The barrier and its resulting cline arise because neutral genes are linked on the chromosomes to the color genes experiencing selection, and can only cross the barrier

after recombination links them to the favored color alleles. The presence of this barrier might seem to indicate that the genetic similarity shown between these taxa is an artifact of history rather than a result of contemporary population processes. However, Barton and Bengtsson (1986; see also Barton 1986) have shown that such a barrier will only slow neutral genes, but cannot stop them for long unless (a) there is very strong selection against intermediate genotypes *and* (b) there are so many genes involved in the characters under selection that recombination will not provide an escape from linked deleterious alleles. Thus, current theory supports the notion that the diagnostic character (color) distinguishing *ivallda* from *stanislaus* should be treated as genetically independent of other potential taxonomic characters — an unreliable indicator in itself of species status or gene flow. A similar lack of congruence between wing characters and electrophoretic data has been found by Porter and Geiger (1988) and Porter and Mattoon (1989) in the Satyrine genus *Coenonympha*. There is no biological inconsistency between the distribution of wing color morphs and our electrophoretic data.

The taxonomy most consistent with the available data recognizes *ivallda* and *stanislaus* as members of the same biological species. The genetic relationship between these taxa and the polytypic *Oeneis chryxus* remains unclear, but we recommend that *ivallda* and *stanislaus* remain classified as subspecies of *Oe. chryxus* pending further study. In the meantime, the evolutionary interpretation of the *ivallda/stanislaus* distribution problem is best addressed from a population biology, rather than community ecology, perspective – that is, the evolutionary ecology and biogeography of individual *ivallda* and *stanislaus* traits should be considered separately.

How convincing is the crypsis scenario? — In the S, which Hovanitz knew best, the geography of substrate color matches *Oeneis* color morph distributions quite well. Slemmons (1966, p. 206) maps the central Sierran andesites; the S limit of the andesite belt is in fact at Tioga Pass, and to the S the alpine is nearly pure granite with some darker volcanic rock in the vicinity of Mammoth Mt. The zone of rapid transition from *stanislaus* to *ivallda* morphs in the S corresponds well to this conspicuous feature of Sierran geology, although detailed mapping of color frequencies remains to be done.

In the N, the alpine zone is more fragmented, and probably not all *Oeneis* populations are known. Most of the northern alpine is, however, on andesite — not granite. There is no corresponding geological feature to account for the reappearance of the *ivallda* morph and the gradual N-ward disappearance of the dark *stanislaus* phenotype. At Carson Pass some 75% of the *Oeneis* habitat is on andesitic mudflows (lahars) of the same character and color as those illustrated by Hovanitz, but the frequency of the *ivallda* morph is high (95%). The rarity of dark and intermediate morphs there strongly suggests that something other than background matching is limiting their N-ward spread: a selection

regime strong enough to produce the sharp cline at Tioga Pass should also favor the *stanislaus* morph at Carson. (It remains possible that the hypothetical predator drops out or switches prey just S of Carson Pass.) There is granitic alpine in the Crystal Range WSW of Lake Tahoe — although it is unlikely that the high frequency of the *ivallda* color morph at Carson Pass could be maintained by massive gene flow from there, this may be the historical source of the three N-most *ivallda* populations (Mt. Lola, Castle-Basin Peaks, Anderson Peak). However, given the inconsistencies in the crypsis scenario for *ivallda* populations in the N (Hovanitz [1940] discussed the tenuousness of crypsis and mimicry hypotheses when experimental data were unavailable), we recommend that it be treated cautiously pending experimental confirmation with a known predator.

Plausibility of an Easterly Invasion by the stanislaus Color Genes — Austin and Murphy (1987) recorded the *ivallda* morph in Nevada only in the Carson Range (Carson City and Washoe Cos.), just a few km E of the Sierra Nevada, and nominate Rocky Mountain univoltine *chryxus* in extreme E Nevada (Elko, Lincoln, White Pine Cos.). Since then *stanislaus* (indistinguishable from Sierran) has been found in the Sweetwater Mts. in Lyon Co. on the California border, again just a few km E of that morph's range in the Sierra Nevada (G. T. Austin, *pers. comm.*). These occurrences seem to be due to W-to-E dispersal from the Sierra, and are uninformative about colonization routes into the Sierra. An absence of relictual *Oeneis* in central Nevada is mirrored in other alpine butterflies, and in other alpine organisms generally (Billings 1978, Harper and Reveal 1978).

The genetic analyses provide no additional characters associated with either *ivallda* or *stanislaus* morphs for comparison to other *chryxus* populations to the N and E, leaving wing color as the only reliable character. All other *chryxus*, and most other *Oeneis*, are colored like *stanislaus*, or even darker (Ferris and Brown 1980). In the absence of a phylogeny for *Oeneis*, we assume that the original invaders of the Sierra were this color and that the *ivallda* color is a uniquely derived autapomorphy. But if the *stanislaus* morph came from the N, why are the relict plesiomorphous color genes in the central Sierra and not also in the N — especially if andesitic substrates are relevant? As Hovanitz noted, the distribution would make more sense if the invasion of the *stanislaus* color genes had come directly across the Great Basin. *Oeneis chryxus* apparently does not occur in Oregon (Dornfeld 1980) or in the Klamath Mts. of N California (Shapiro et al. 1981), reaching its southern limit (W of the Rockies) in Washington. Its range as mapped by Scott (1986, p. 248) raises a very serious question of where an invasion from the N might have come from; no relicts of the hypothetical N route have been found.

At least one other butterfly taxon is distributed along the hypothetical NE invasion route. *Limenitis lorquini weidemeyerii* (Edwards), a Rocky Mountain middle-elevation nymphalid butterfly, is restricted to

montane riparian canyon habitats in the Great Basin (Austin and Murphy 1987; Porter 1989). Its distribution closely follows the colonization route in the Humboldt drainage proposed by Major and Bamberg (1967): it crosses the low-elevation desert into the Wassuk Mts. and reaches its W distribution limits on the N shore of Mono Lake (see Fig. 1), where it hybridizes with the Sierran *L. lorquini lorquini* (Boisduval) (Porter 1989). "Pure" *L. l. weidemeyerii* and hybrid wing pattern morphs are sympatric with *Oe. c. stanislaus* near Sonora Pass where montane and subalpine habitats interdigitate. The distribution of the *weidemeyerii* morph is entirely consistent with an invasion of *stanislaus* color genes from the E into the central Sierra. The presence of *L. lorquini burrisoni* Maynard (a weakly defined taxon quite similar in phenotype to nominate *lorquini*) in Oregon, Washington and into western Montana makes a northerly route of Sierran invasion by the *weidemeyerii* form seem highly unlikely. Although *Limenitis* is found in montane habitats and *Oeneis* rarely strays from the alpine, similar immigration corridors may have been used at different times by both.

The simplest scenario consistent with the *Oeneis* distribution data has *chryxus* invading first (from the N or E) and evolving the distinctive *ivallda* color, with a second *chryxus* invasion from the E injecting the distinctive *stanislaus* color into the central Sierran populations. However, this is by no means the only available scenario, and it is even possible that the butterscotch brown of the *stanislaus* morph represents a character reversal, and not evidence of two Sierran invasions. Genetic studies of the entire *Oeneis chryxus* complex in western North America, with an eye towards alleles linking Sierran and potential source populations, may expose characters which will help resolve the biogeographical problem. The answer will be of considerable value in the interpretation of the origins of the entire Sierran alpine biotic community.

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